

Justifications for the extra assumptions of studying the predator-prey interaction with Maximum Entropy Resource Allocation (MERA)

Jade, Dec 15

In this write-up I introduce and justify two additional assumptions to explore the predator-prey interaction with MERA other than the original assumptions. After that, a general framework for theoretical and simulation analysis is sketched.

1 The constraint for the predator

The basic logic of applying MERA to study the predator-prey interaction is simple: just take prey individuals as resources and allocate them among the predator individuals. However, as will be shown in the following, certain things have to be further specified to get a meaningful result.

In the previous framework of MERA, a constraint on resource use is set so that all available resource must be utilized by the species. Here it is obvious that the same constraint cannot be applied to the predator-prey

scenario. This is because unlike the previous resource which is replenished to a constant amount at each step, the amount of prey available each time does change with the predator's consumption. Therefore, prey abundance could potentially drop to zero, which leads to extinction of both species.

Here using a thought experiment with simple derivations, I am going to prove that 1) there must be a constraint on prey consumption and 2) if the constraint is a constant, it equals the net growth rate of prey at equilibrium, and 3) for the equilibrium to be stable, prey growth rate must be a negative function of its abundance.

First recall that according to the MERA assumptions, the prey that can be consumed by the predator range from 0 to $2N_{predator}$ (assuming $\theta_{predator} = 1$). If there is no constraint on prey consumption, when there are plenty of prey individuals ($N_{prey} > 2N_{predator}$), the predator will keep growing to its capacity, i.e. abundance is doubled in each step. Notice that the prey abundance is constrained by the resource available, so with the predator abundance growing, eventually $N_{prey} < 2N_{predator}$. At this point, the predator will wipe out the prey and both species go extinct. Therefore, there must be a constraint for the predator on its consumption of the prey, which prevents it from growing to its highest capacity.

Same as all systems, the equilibrium condition for the predator-prey interaction is simply

$$\frac{dN_{predator}}{dt} = \frac{dN_{prey}}{dt} = 0 \quad (1)$$

Under the MERA assumptions, for $\frac{dN_{predator}}{dt}$ to be zero, the number of prey (which is analogous to the previous resource) consumed $R_{predator}$ has to equal $N_{predator}$ (assuming $\theta_{predator} = 1$).

$$N_{predator}^e = R_{predator} \quad (2)$$

The superscript e indicates that the value is that of the variable at equilibrium. For $\frac{dN_{prey}}{dt}$, it can also be expressed by

$$\frac{dN_{prey}}{dt}(N) = g_{prey}(N) - R_{predator} \quad (3)$$

where $g_{prey}(N)$ is the net growth rate of prey before predation. Combining the above, we can derive that at equilibrium,

$$g_{prey}(N^e) = R_{predator} = N_{predator}^e \quad (4)$$

This is the constraint for the predator, which means that instead of the total abundance, **the predator is constrained to consume the net growth rate of prey at equilibrium.**

Now let's look at the stability of this equilibrium. Suppose that a perturbation causes the prey abundance to drop below the equilibrium level to $N'_{prey} < N_{prey}^e$. The net growth of prey at this point is $g_{prey}(N')$.

Therefore

$$\frac{dN_{prey}}{dt}(N') = g_{prey}(N') - R_{predator} \quad (5)$$

Notice that the second term is the constraint on predator, which is still equal to $g_{prey}(N^e)$. For the equilibrium to be stable, this derivative

$\frac{dN_{prey}}{dt}(N')$ must be positive so that the population can grow back to N_{prey}^e .

Therefore

$$g_{prey}(N') - R_{predator} = g_{prey}(N') - g_{prey}(N^e) > 0 \quad (6)$$

$$g_{prey}(N') > g_{prey}(N) \quad (7)$$

Similarly we can prove that if the perturbation causes N_{prey} to increase ($N'_{prey} > N_{prey}^e$), the resulting $g_{prey}(N')$ has to be smaller than $g_{prey}(N^e)$ to drag the system back to equilibrium. This means that **for this system to be stable, the net growth rate of prey has to be a negative function of abundance around the equilibrium. In the case where it does not hold universally, the equilibrium is only locally stable in the range where net growth rate is a negative function of abundance.**

1.1 Growth as a function of abundance in MERA

We know that in the exponential growth function, net growth rate $\frac{dN}{dt}$ is a positive function of N , therefore the prey cannot follow the exponential growth function for the predator-prey interaction described by MERA to have a stable equilibrium. In the logistic growth function, $\frac{dN}{dt}$ is a positive function of N when $N < K/2$, therefore the MERA predator-prey interaction is only stable when $N_{prey} > K/2$ if the prey follows the logistic growth function. Now let's look at the case where the prey growth is described by MERA.

Notice that in the current MERA framework, resource is constrained to be fully consumed by the prey, therefore N_{prey} cannot be smaller than $R/2\theta_{prey}$. When the prey is the only species consuming the resource, the following shows how growth rate changes as a function of abundance ($R = 100, \theta_{prey} = 1$):

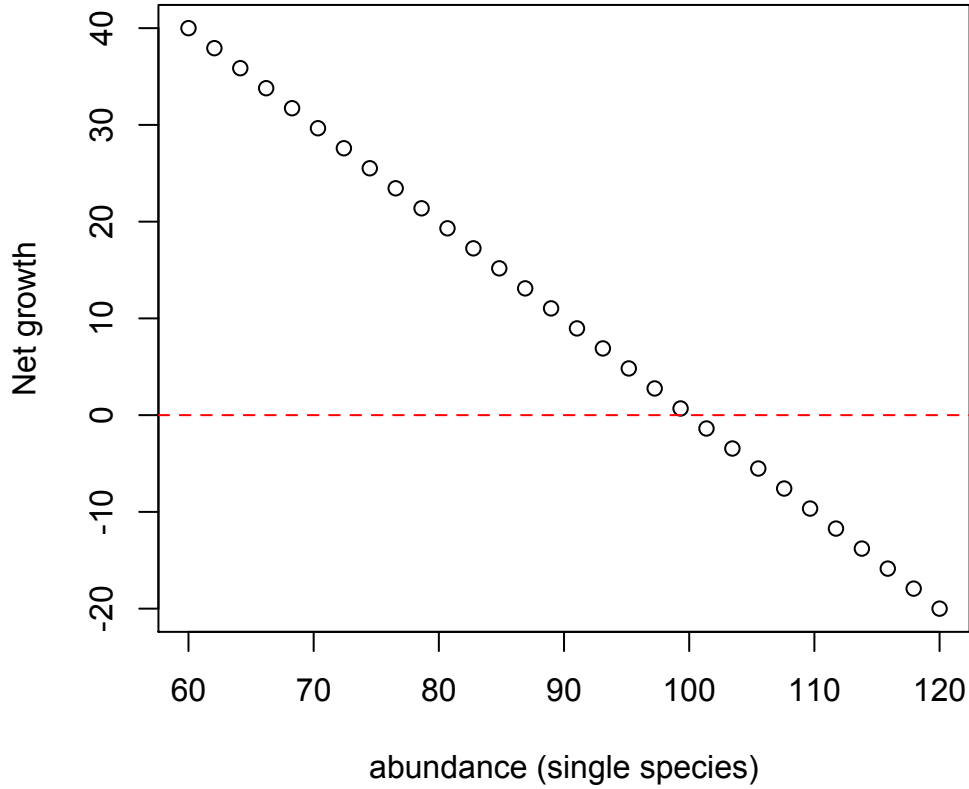


Figure. 1

In this special case, the line above can be analytically described by

$$g_{prey}(N) = R/\theta_{prey} - N_{prey} \quad (8)$$

$$(N_{prey} \geq R/2\theta_{prey})$$

where the first term is the equilibrium abundance of prey without predation. D_r does not enter the function. Apparently the predator-prey interaction is stable in the single prey species scenario, as long as the predator has a predation constraint $R_{predator}$ that is smaller than $R/2\theta_{prey}$, which is the highest net growth rate possible for the prey.

When there is one more species other than the prey that is competing for the resource (but is itself not a prey), however, the pattern is more complicated. First of all, both $D_{r,predator}$ and $D_{r,prey}$ influence the pattern:

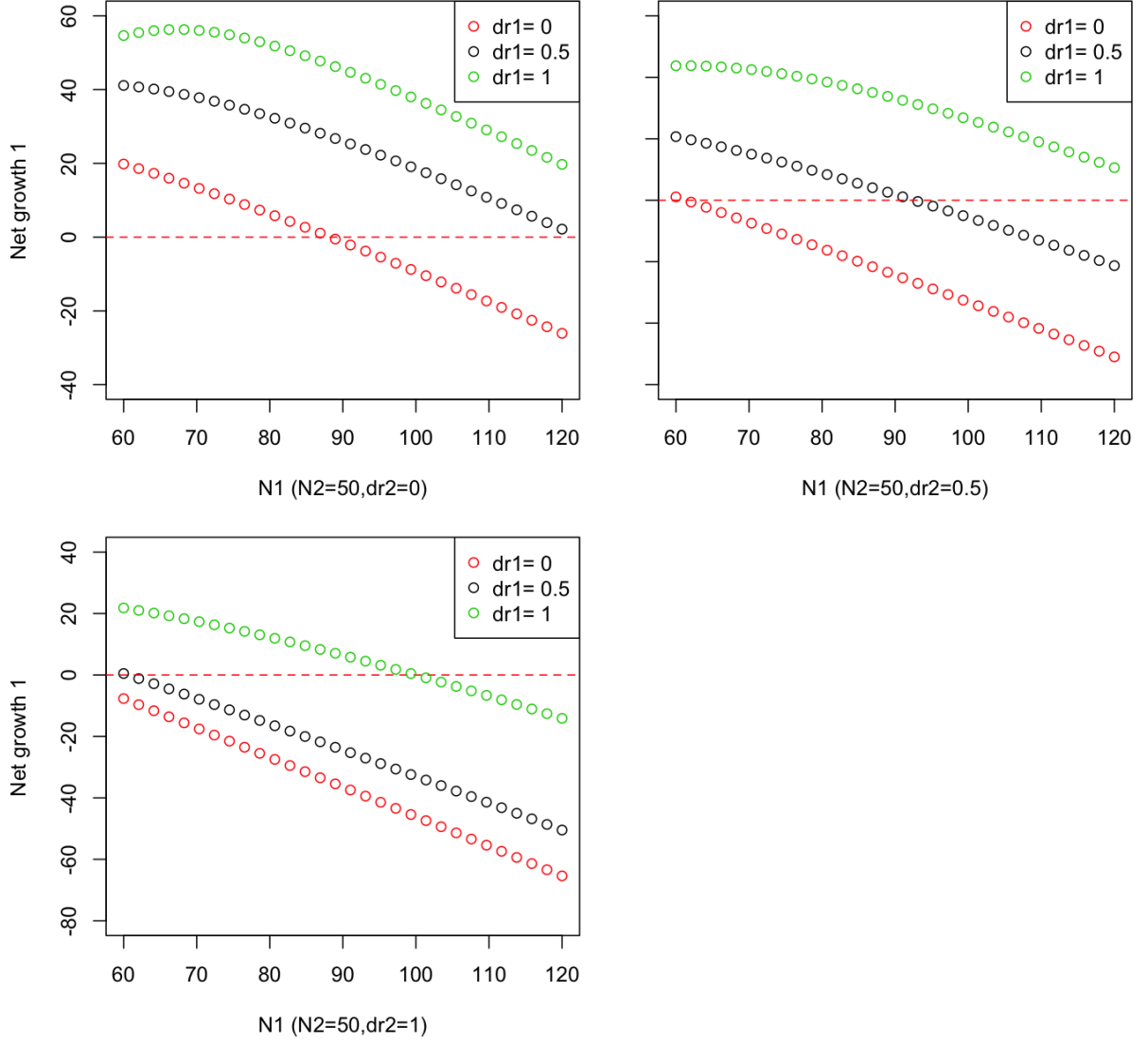


Figure. 2

In the graph D_{r1} stands for $D_{r,predator}$ and D_{r2} stands for $D_{r,prey}$. We can see that when $D_{r,predator} = 1$, $D_{r,prey} = 0$, net growth slightly increases with abundance before decreasing, which means the predator-prey equilibrium might not be universally stable in this scenario.

In conclusion, MERA predicts the net growth rate to be a negative function of abundance at least for some intervals, which means that it is possible to get a stable equilibrium by describing the predator-prey interaction and prey growth with MERA simultaneously.

2 *Finding an exact value for the $R_{predator}$

We have proved that with the additional assumption justified in section 1, MERA could predict a stable equilibrium for the predator-prey interaction and prey growth. There is only one more question: how is the constraint for the predator determined? We know that as long as the constraint $R_{predator}$ falls within the interval where g_{prey} is a negative function of N_{prey} , it could result in an at least locally stable equilibrium. But the MERA procedure cannot be applied unless we have an exact value for $R_{predator}$. About this I have an attempted thought based on fishing economics, assuming that the predator is always aiming for the largest population possible given the constraints on fundamental resources.

Suppose that the predator is like an experienced fisherman and is familiar with the growth pattern of the prey. For an optimal outcome, undoubtedly the predator will choose to maintain the prey at a level corresponding to the highest growth rate (close to $R/2\theta_{prey}$ in the graphs above). In this way the predator can maintain a highest population size at a stable equilibrium.

This assumption sounds straightforward but gets very complicated easily as the number of preys increases. In the case where there are two preys competing for the same fundamental resource and are both potential food source for the predator, the predator will have to figure out a optimization problem as is shown in the graph:

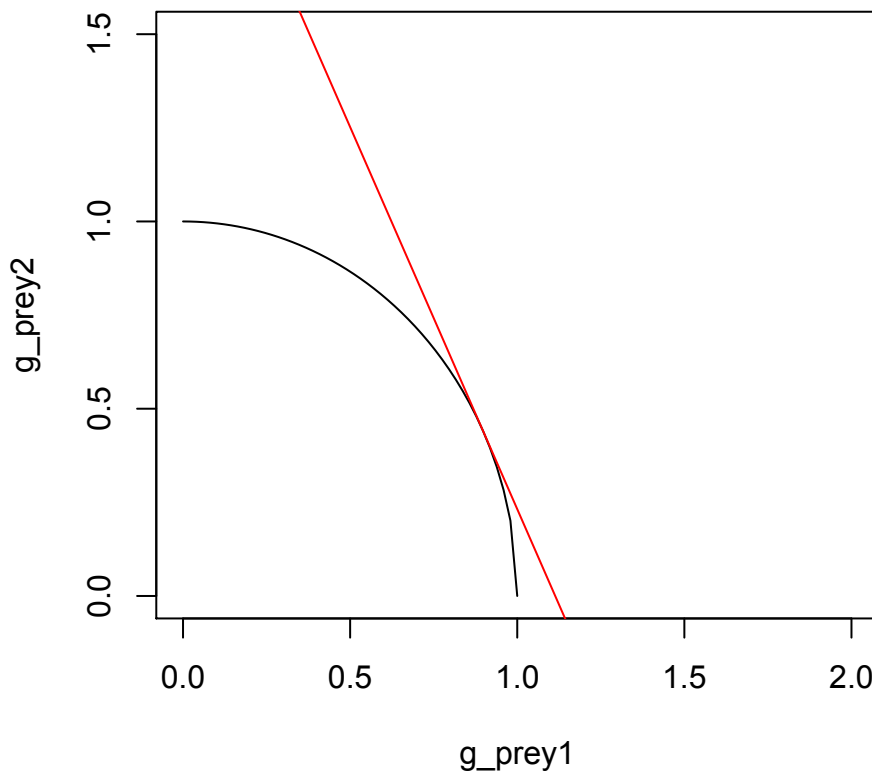


Figure. 3

The black curve is all possible growth rate combinations between the two preys given the resource constraint (in economics it is called the productivity possibility frontier). The red straight line is the objective

function that the predator is trying to maximize

$$\begin{aligned}
N_{predator}^e &= \frac{R_{predator,1}}{\theta_{predator,1}} + \frac{R_{predator,2}}{\theta_{predator,2}} \\
&= \frac{g_{prey1}}{\theta_{predator,1}} + \frac{g_{prey2}}{\theta_{predator,2}}
\end{aligned} \tag{9}$$

$\theta_{predator,i}$ is the number of the i th prey that a predator individual needs to maintain itself (and twice the amount to reproduce). The optimal predation level is given by the tangent between the objective function and the productivity possibility frontier. With the number of prey species increasing, the problem becomes a multi-dimension linear programming problem for the predator. Moreover, if there are more than one predators feeding on the same group of preys, the objective functions can be different, which means that the actual constraint might be in-between the scenarios where there is only one predator, or the predators are facing different constraints. I haven't thought of a satisfying answer to this. However it is clear that an analytical solution to the MERA equations (even just at equilibrium) will help resolve this conundrum, which I am still working on and hopefully will be included in the next write-up.

3 Analytical framework for predator-prey interaction

In this section I made a sketchy outline of what we might do to examine the implications of MERA on the predator-prey interaction under three general

scenarios: one prey and one predator, two (more than one) preys and two (more than one) predators.

3.1 One prey and one predator

This is the simplest possible scenario where the constraint for the predator is just the highest possible growth rate of the prey (close to $R/2\theta_{prey}$) and the equilibrium predator abundance is just this constraint divided by $\theta_{predator}$. A slightly more complicated but interesting scenario is the one with an extra species competing for resource with the prey, which is itself not a prey to the predator. The effect of the parameters of this extra species on the predator's constraint strategy and equilibrium abundances of the predator-prey pair can be examined.

3.2 Two preys and one predator

In this case the predator chooses its constraints using the optimizing strategy illustrated in Fig.3. The top-down effect of $\theta_{predator}$ and bottom-up effect of θ_{prey} and $D_{r,prey}$ s and their interactions on the equilibrium can be examined.

3.3 Two predators

When there is only one prey, the optimum condition is the same for the two predators and the prey is constrained at the abundance corresponding to its highest growth rate. The effect of an extra non-prey species competing for resource with the prey can be examined.

When there are more than one prey, the objective functions for the two predators can be different. As a first step, however, we can assume that the slope of the objective functions (the slope of the red line in Fig.3) is the same:

$$\frac{\theta_{11}}{\theta_{12}} = \frac{\theta_{21}}{\theta_{22}} \quad (10)$$

θ_{ij} is the maintenance requirement of the j th prey for the i th predator. The above equation suggests that relative requirement between the preys is the same for the two predators, which is to a certain extent reasonable: the energy condense prey is always energy condense, despite the energy requirement of the predator. With this extra assumption, the constraints for the predators can be unambiguously determined as is illustrated in Fig.3. Using the equations from the last write-up ("Extending the theory to two resources"), the top-down and bottom-up effects of the predator and prey parameters on the equilibrium abundances and feeding preferences can be examined.